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ANATOMY AND HISTOLOGY OF THE MALE REPRODUCTIVE SYSTEM IN THE ADULT AND PUPA OF THE DORYLINE ANT, *AENICTUS GRACILIS* EMERY (HYMENOPTERA: FORMICIDAE)

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Abstract.—This paper presents the anatomy and histology of the reproductive system, the external genitalia, and the terminal gastric sterna in the male adult and advanced-stage pupa of the Old World doryline ant, *Aenictus gracilis.* The male reproductive system consists of the testes, the vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the short bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia. The testes are enclosed in a thin common capsule, and each testis is composed of about 32 follicles. The epithelium of the testicular follicle in the adult consiss of a basal and an inner layer of cells around a central lumen, which contains scattered or clustered spermatozoa. In the pupa, the epithelium is composed of irregularly-shaped cells, each with a large central vacuole filled with spermatozoa. The seminal vesicles are U-shaped in the adult and pupa. The epithelial cells in the pupa are taller than those in the adult. In the adult, spermatozoa were present throughout, but in the pupa, sperm were absent throughout. The accessory glands are tubular and bent around the proximal region of the intestine. The epithelium is more folded in the pupa than in the adult. In the adult, some regions contain an acidophilic secretion, some basophilic, and some both. In the ejaculatory duct, a cuticular wedge is present on the lateral and ventral walls; this wedge is more complex in its structure in the adult. The duct enters the dorsal, posterior surface of the aedeagal bladder. The epithelium of the bladder consists of small cells covered by a thick, wrinkled intima. The muscle fibers that surround the bladder are larger in diameter than the visceral muscles of the ejaculatory duct. The lumen of the bladder is devoid of secretion. The basal ring of the genitalia, the three pairs of valves, and the eighth and ninth sterna are described. They are quite different in shape from those of the New World dorylines, *Eciton hamatum* and *Neivamyrmex harrisi,* but in some respects resemble those of the Old World dorylines, *Dorylus wilverthi* and *nigricans.* Comparisons made with previously described Old and New World species have revealed structures and features that lend support to the concept of the triphyletic origin of the dorylines.

A review of the studies on the male reproductive system in ants was made by Forbes (1954), and further information has been added by Hung and Vinson (1975). The study of the male reproductive system in doryline ants was pioneered by Mukerjee (1926), who described the anatomy of this system in the Old World *Dorylus labiatus.* Descriptions of the anatomy and histology of this system that followed are those of *Eciton hamatum* (Forbes, 1958), *Neivamyrmex harrisi* (Forbes and Do-Van-Quy, 1965), *Dorylus wilverthi*

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and *D. nigricans* (Ford and Forbes, 1980, 1983). The morphology of the male internal reproductive system for representative species of Old and New World army ants has been described by Gotwald and Burdette (1981) to interpret phylogenetic implications of this morphology. After Clausen's work (1938), the genitalic valves have been studied in detail and used as the basis for the classification of ants even to the subspecies level (Forbes, 1952; Borgmeier, 1955; Krafchick, 1959).

This is the first anatomical and histological description of the reproductive system of the male adult and advanced-stage pupa of the Old World doryline *Aenictus gracilis.* Comparisons are made with an African *Aenictus* sp. (Gotwald and Burdette, 1981) and with other dorylines previously described.

The specimens and methods used in this study were those reported in the description of the male digestive system of this ant (Shyamalanath and Forbes, 1980).

OBSERVATIONS AND DISCUSSION

Anatomy of the reproductive system. This system in the male adult and pupa consists of the testes, the vasa efferentia, the vasa deferentia, the seminal vesicles, the accessory glands, the short bound accessory gland duct, the ejaculatory duct and wedge, the aedeagal bladder, and the external genitalia (Fig. 1).

The testes are enclosed within a very thin, common testicular capsule and lie in a concavity on the dorsal, posterior half of the ventriculus from the middle of the 4th to the end of the 5th abdominal segments. Each testis is composed of about 32 slender follicles, which are longer in the pupa than in the adult. The tubules of each testis form a compact mass, and their anterior ends converge medially. The posterior end of each follicle leads into a short narrow duct, the vas efferens. The vasa efferentia of each testis unite to form the short, wider vas deferens. The distal end of the vas deferens is slightly constricted where it leads into a dilated, elongated, U-shaped tube, the seminal vesicle, situated along the outer margin of the testis. The first part of the seminal vesicle is convoluted only in the adult and lies beneath the posterior region of the testis. The proximal arm of the seminal vesicle lies beneath the distal one, and both arms are covered with the testicular capsule. The distal arm of the seminal vesicle continues backward, emerges from the capsule, and opens into the accessory gland at about the middle of its lateral margin. The seminal vesicle in the pupa is narrower than that in the adult. The tubular-shaped accessory glands are bent around the proximal region of the intestine and unite beneath it to form a short bound accessory gland duct that continues into the ejaculatory duct with the wedge. The ejaculatory duct opens into the dorsal surface of a thick-walled aedeagal bladder situated beneath the bound accessory gland duct and the ejaculatory

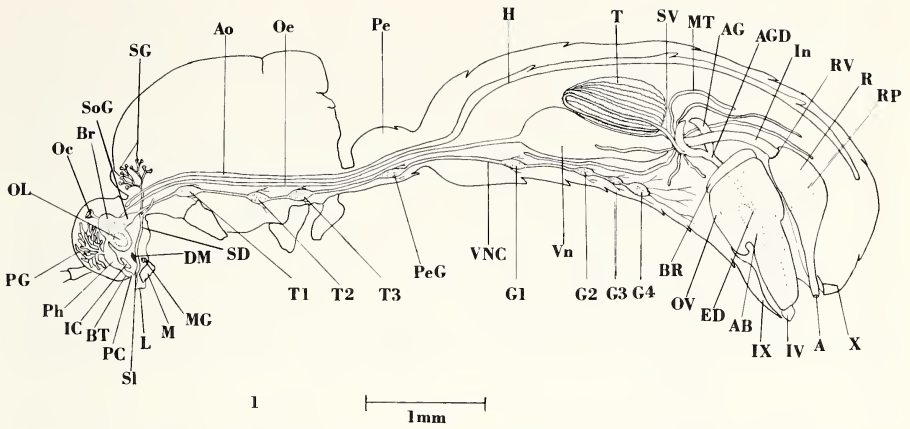

Fig. 1. Diagram of a lateral dissection of the adult male of *A. gracilis.* (From the original of Fig. 1, S. Shyamalanath and J. Forbes, J. New York Entomol. Soc. 88:18.)

duct. The posterior region of the aedeagal bladder lies between the median walls of the inner genitalic valves and opens to the outside near the ends of these valves. The aedaegal bladder in the pupa is larger and has a more spacious lumen than that in the adult.

The anatomy of the reproduction system of *A. gracilis* bears a close resemblance to that of an African *Aenictus* sp. (Gotwald and Burdette, 1981), except that the testes were absent in the adult of the African species; these authors also reported that testes were absent in the adults of some species of the subfamilies Ecitoninae and Dorylinae. The reduction in the length of the testicular follicles in the adult of *A. gracilis* from the length of the follicles in the pupa could be indicative of the shrinking and eventual total atrophy. *A. gracilis* with about 32 testicular follicles resembles the Old World dorylines that have comparatively more follicles, 35–40 in the adult and pupa of *Dorylus wilverthi,* 50–55 in the pupa of *D. nigricans* (Ford and Forbes, 1980), and a fair number in *D. labiatus* (Mukerjee, 1926). The New World *Eciton hamatum* has 20 follicles (Forbes, 1958) and *Neivamyrmex harrisi* 22–25 (Forbes and Do-Van-Quy, 1965). The common capsule surrounding the testes of *A. gracilis* is similar to that in *N. harrisi,* but no capsule covers the testes of *D. wilverthi, nigricans,* or *labiatus.* In general arrangement the seminal vesicles resemble those of the other dorylines. However, structures comparable to the collecting sac at the anterior end of the seminal duct and the dilated vesicula seminalis at the posterior end, reported to be present in *D. labiatus,* are not present in *A. gracilis.* The accessory glands of *A. gracilis* and the African *Aenictus* sp. are short, curved glands, which resemble those of *D. labiatus* in shape. These glands in *D. wilverthi* and *nigricans* are thick

walled, S-shaped tubes and in *E. hamatum* and *N. harrisi* are tightly coiled tubes situated on either side of the intestine. The bound accessory gland duct is short and straight in the Old World dorylines, while in the New World dorylines it is much longer and in *E. hamatum* it encircles the ventriculus 5 or 6 times. The ejaculatory duct in all the dorylines examined opens into the dorsal, posterior end of the aedaegal bladder. The blind diverticulum found on the dorsal side of this duct by Mukerjee (1926) in a male of *D. labiatus* has not been seen in any other doryline examined or reported. The aedeagal bladder found in *A. gracilis* is present in *D. wilverthi* and *nigricans,* in *E. hamatum* and *N. harrisi.* It was not reported in *D. labiatus* nor in any of the army ants investigated by Gotwald and Burdette (1981).

EXTERNAL GENITALIA AND TERMINAL GASTRIC STERNA

The external genitalia are composed of a basal ring and 3 pairs of valves, the outer, the middle, and the inner, all of which are sclerotized. They are retracted into the genital chamber and only the distal ends of the outer and inner valves protrude beyond the posterior margin of the gaster (Fig. 1). The basal ring or lamina annularis is ring-shaped and situated in the posterior half of the 6th abdominal segment. Its anterior margin is attached to the reflected intersegmental membranes of the 9th segment. The dorsal surface of the basal ring is the broadest, its anterior margin is heavily sclerotized, and there is a distinct median process. Behind this median process there is a thin, nonsclerotized, V-shaped region that appears as a notch (Fig. 2). The outer valves or parameres are situated dorsally and laterally behind the basal ring to which they are attached by a thin membrane. Each has a broad anterior region, the lamina parameralis, and a narrow, finger-like posterior region, the paramere. The outer surface of both these regions is convex, and there is no suture or demarcation between the two regions; both regions are uniformly sclerotized. Ventrolaterally at the base of the paramere, there is a distinct indentation (Fig. 3). The laminae paramerales lie close to each other along the middorsal line, and ventrally their anterior halves are held together by a thick, nonsclerotized membrane. The parameres are separated

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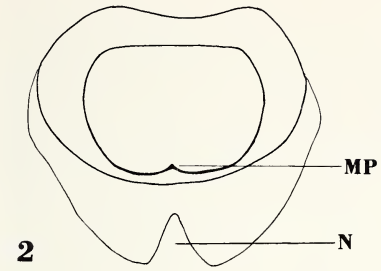
Figs. 2–7. Genitalic valves and terminal gastric sterna of the adult male of *A. gracilis.* All figures are drawn to the same scale. 2. Diagram of an anterodorsal view of the basal ring, the lamina annularis. The dorsal side is downward in this drawing. 3. Diagram of a lateral view of the right outer genitalic valve, the paramere. 4. Diagram of a lateral view of the right middle genitalic valve, the volsellaris, attached to an inner part of the lamina parameralis of the outer valve. 5. Diagram of a lateral view of the right inner genitalic valve, the lamina aedeagalis. 6. Diagram of a ventral view of the IXth abdominal sternum, the subgenital plate. Dotted lines indicate the margins of its dorsal plate. 7. Diagram of a ventral view of the VIIIth sternum.



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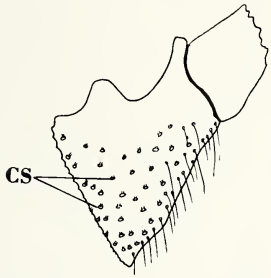

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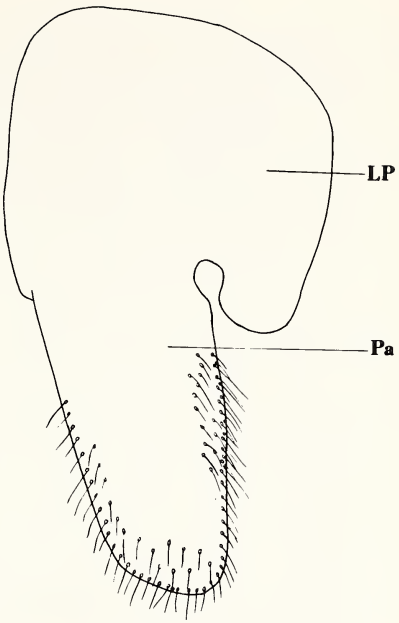

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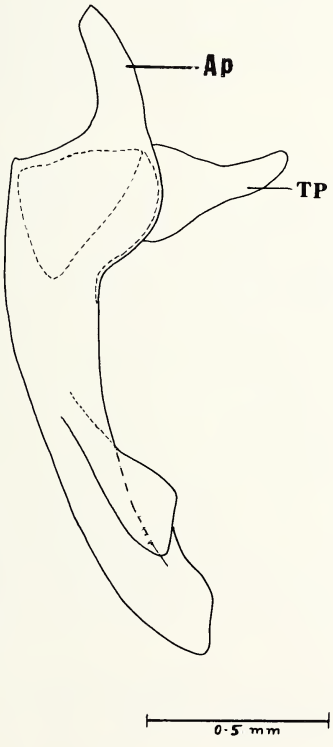

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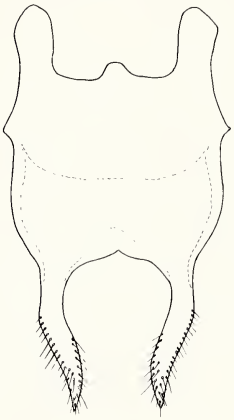

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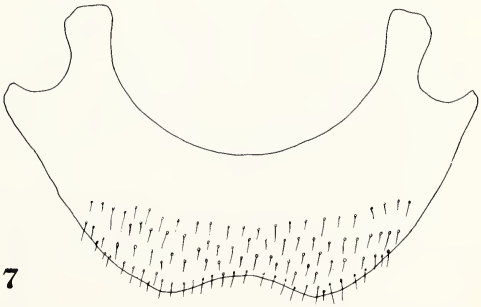

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from each other. Many sensory hairs are present along the upper and lower margins of the parameres, and some are present on their median surfaces. The middle valves or volsellares are the smallest of the valves and the most heavily sclerotized. Each is roughly quadrilateral in shape and is strongly attached along its anteroventral margin to the ventroposterior margin of the lamina parameralis (Fig. 4). It lies mediad of the paramere and is inflected upward. Campaniform sensilla are present on the posterior surfaces, and sensory hairs are only on the ventroposterior margin. The inner valves or laminae aedeagales constitute the male intromittent organ. These are moderately sclerotized, narrow, elongated valves lying close to each other. The posterior half in lateral view is bent downward. When viewed dorsally and ventrally, they are broader anteriorly and posteriorly and narrower in the midregion (Fig. 5). The dorsal and ventral inner margins of these valves are joined by thin membranes enclosing a narrow space that opens to the outside by a terminal orifice. The dorsal membrane is the spatha. Wavy flaps from the lateral margins of the posterior region fold ventrally and form a short ventral trough. The anterior ventral margins of the two valves are attached to the posterior half of the lateral sides of a triangular plate. The base of this plate is attached to the posterior margin of the membrane extending between the ventral anterior halves of the laminae paramerales. This plate is less sclerotized than the inner valves. Proximally, the aedeagus has a pair of anterodorsally directed arms, the aedeagal apodemes. These valves are devoid of sensilla or sensory hairs.

The IXth sternum or subgenital plate is located on the floor of the genital chamber. It has a broad, shield-shaped body that terminates in two widely separated processes, and this segment is heavily sclerotized (Fig. 6). The body consists of a dorsal and ventral plate fused along their lateral margins. The dorsal plate extends up to half the length of the ventral plate. The forward margin of the ventral plate has three anteriorly directed apodemes; the middle one is the shortest. Sensory hairs are found on the posterolateral regions of the body of this plate and on the terminal processes. The VIIIth sternum forms the anterior floor of the genital chamber, and it is roughly crescent-shaped (Fig. 7). The anterior margin has a pair of lateral arms, and the segment is heavily sclerotized between them. The posterior margin has a shallow notch in its midregion. Sensory hairs are present on its ventral posterior half. The external genitalia and terminal gastric sterna of the pupa are similar in all respects to those of the adult except that the component parts are less sclerotized.

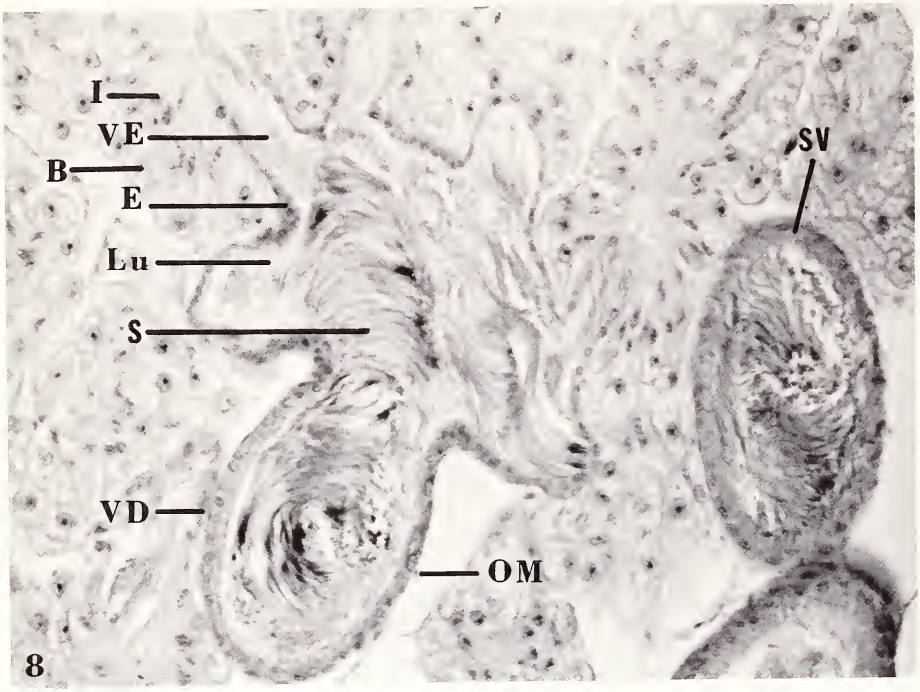
The external genitalia of *A. gracilis* conform to the doryline pattern in general organization and resemble those of the Old World dorylines, *D. wilverthi* and *nigricans* (Ford and Forbes, 1980). The shapes of the component parts are strikingly different from those of the New World dorylines, *E. hamatum* (Forbes, 1958) and *N. harrisi* (Forbes and Do-Van-Quy, 1965).

While the basal ring of *A. gracilis* resembles that of the African dorylines, *D. wilverthi* and *D. nigricans,* it has a sclerotized median process on the anterior margin of the dorsal surface and a posteriorly directed notch behind this process. The middorsal apodeme present on the ventral part of the basal ring of *D. wilverthi* and *D. nigricans* is absent in *A. gracilis.* Also, the outer valves of *A. gracilis* are not fused to the basal ring along their dorsal, anterior borders as they are in *D. wilverthi* and *nigricans.* The middle valves of *A. gracilis* are broad and roughly quadrilateral in shape while those of *D. wilverthi* and *nigricans* are finger-shaped. These valves of *A. gracilis* are strongly attached to the inner surfaces of the outer valves; this is not the arrangement in *D. wilverthi* and *D. nigricans.* The presence of many campaniform sensilla on the posterior surfaces of the middle valves of *A. gracilis* has not been reported in other dorylines. The shapes of the inner valves of all the dorylines described, the Old World as well as the New, are distinctly different. The presence of the triangular plate at the anteroventral margins of the inner valves is characteristic of *A. gracilis.* The IXth sternum is considered an integral part of the genitalia because it provides muscle attachment (Krafchick, 1959). In general shape, the IXth sternum of *A. gracilis* resembles that of other dorylines (Borgmeier, 1955; Forbes, 1958; Forbes and Do-Van-Quy, 1965; Ford and Forbes, 1980).

HISTOLOGY OF THE REPRODUCTIVE SYSTEM

The testicular capsule in the adult is a network of interlacing tracheae of varying diameters, and it continues inward between the testicular follicles. Fat cells are found on the surface of the capsule. In the pupa, the capsule is not as well formed; the tracheae are smaller and fewer. The epithelium of the testicular follicles in the adult consists of a basal layer and an inner layer of cells arranged around a central lumen (Fig. 8). The larger cuboidal or pyramidal cells of the basal layer have distinct cell boundaries. The cytoplasm of these cells is granular and highly vacuolated, and a large, ellipsoidal nucleus is located in the basal region. The smaller cells of the inner layer are without distinct cell boundaries. They have densely granular cytoplasm and small oval nuclei. The central lumen has clusters of spermatozoa or scattered spermatozoa and their tails extend into the cytoplasm of the basal cell layer. This arrangement of the testicular epithlium resembles that in the adult and pupa of *D. wilverthi* and in the pupa of *D. nigricans* (Ford and Forbes, 1983). In the pupa, large irregularly-shaped cells form the epithelium of the follicles and there is no central lumen. The cytoplasm is restricted to the periphery of the cells and encloses a large vacuole that is filled with spermatozoa (Fig. 9). This condition has not been reported in any of the other dorylines.

The epithelium of each vas efferens in the adult is a continuation of the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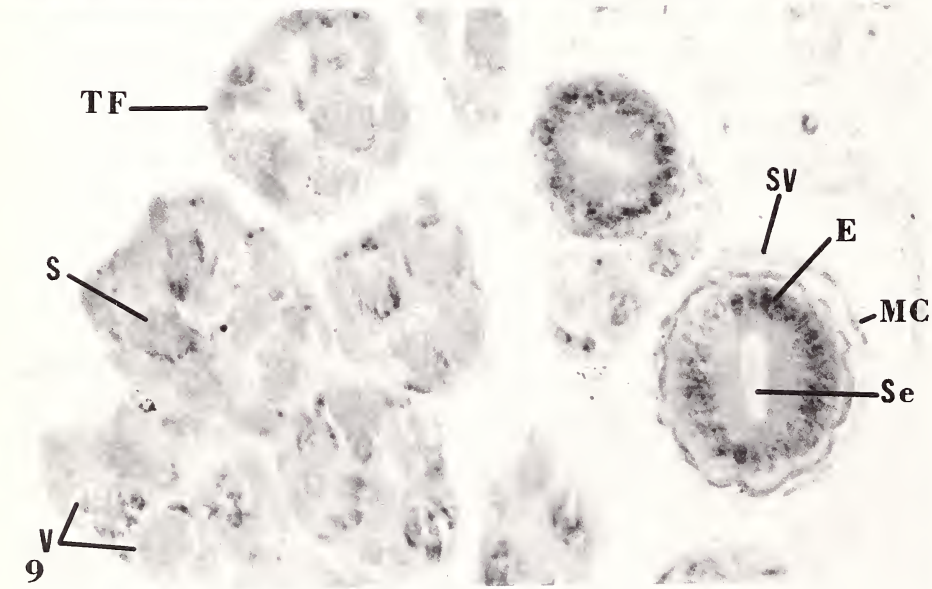
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basal epithelial layer of the testicular follicle. These basal cells decrease abruptly in size and become low and cuboidal in shape (Fig. 8). The nuclei are centrally located. The lumina of the vasa efferentia contain scattered or clustered spermatozoa. In the pupa, the cells of these organs are low and columnar with oval, basally located nuclei and basophilic cytoplasm. The lumina of the vasa efferentia are narrower than those of the adult and are devoid of spermatozoa, but they do contain a fine-granular, neutrophilic secretion that arises from the free surface of the cells.

The epithelial cells of the vas deferens of the adult are larger than those of the vasa efferentia, and the epithelium of the vas deferens is surrounded by a thin layer of small, obliquely arranged muscle fibers. The lumen contains scattered spermatozoa (Fig. 8). In the pupa the single layer of epithelial cells of this organ is taller than that lining the vasa efferentia, and the cytoplasm is still basophilic in its staining reaction. The lumen is narrower, is devoid of spermatozoa and has a secretion similar to that found in the vasa efferentia.

In the seminal vesicles, the epithelium is gradually transformed from the cuboidal cells of the vas deferens to low columnar. The cytoplasm is granular, and some vacuoles are present. Each cell has a basally located, ellipsoidal nucleus; the long axis of the nucleus is parallel to the basement membrane. A small amount of neutrophilic-staining, granular secretion was seen on the free surface of some of the cells (Fig. 8). The muscle coat gradually becomes thicker from the proximal to the distal region of this organ. In the narrow duct at the posterior end of the seminal vesicle, the epithelium increases slightly in height and the nuclei change their position to lie at right angles to the basement membrane. This position of the nuclei continues into the accessory glands. The lumen of this organ is filled with spermatozoa except in one adult where the sperm were confined to the testicular follicles. Spermatozoa were never found in the distal narrow duct (Fig. 10). In the pupa the epithelium consists of a single layer of tall columnar cells that almost occlude the lumen. The cytoplasm is more granular, basophilic and with fewer vacuoles. The lumen is filled with coarser granules that are less basophilic than those in the cytoplasm and no spermatozoa are present (Fig. 9).

The histology of the seminal vesicle and the distribution of spermatozoa are similar in the adults of the dorylines described. Variations in the secretions of this gland have been reported: In *N. harrisi* (Forbes and Do-Van-Quy, 1965) the secretion is granular and acidophilic in the constricted ter-

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Figs. 8, 9. Photomicrographs of sections through the testes of *A. gracilis*. 8. Adult testis that shows testicular follicles, vasa efferentia, vas deferens, and seminal vesicle. ×275. 9. Pupal testis that shows follicles and seminal vesicle. ×600.

minal region; in *D. wilverthi* and *nigricans* there is mixing of both acidophilic and basophilic secretions in the anterior region and basophilic in the posterior.

The epithelium of the accessory glands in the adult is folded and the cells vary in height from low cuboidal to tall columnar. The cytoplasm is granular and slightly vacuolate. The secretion in the dorsal half of the gland is distinctly acidophilic and is composed of coarse spherical granules that are formed in the supranuclear region of the cells (Fig. 10). The cells become packed with this secretion, the surface membrane of the cells disintegrates, and the secretion is discharged into the lumen. Only a thin basal layer of cytoplasm containing the nuclei remains of these epithelial cells that elaborated this secretion. In the ventral half of the gland, the secretion is acidophilic toward the median wall, basophilic toward the lateral wall, and a combination of both in the center of the lumen. The basophilic secretion, in contrast to the acidophilic, is developed within the cytoplasm of the entire cell and consists of small, fine granules concentrated in the upper ends of the cells and is discharged through the surface membrane into the lumen. The muscle coat is composed of an inner layer of 3 or 4 oblique fibers, 1 or 2 of which extend into the epithelial folds, and an outer layer of 2 or 3 circular fibers (Fig. 10). In the pupa the epithelium consists of a single layer of columnar cells that vary in height and is more folded than in the adult. These folds almost occlude the lumen. The cytoplasm is fine-granular throughout the cells but more dense in the supranuclear regions. A small amount of neutral staining secretion is present in the lumen.

Spermatozoa are normally absent in these glands, but their unusual presence has been reported at the anterior ends of these glands in the adults of *D. nigricans* (Ford and Forbes, 1983) and in limited areas in these glands in the subgenus *Rhogmus* (Gotwald and Burdette, 1981).

The accessory gland ducts are wider proximally, and their epithelial cells vary in height from cuboidal to columnar. In the adult, where each accessory gland enters its duct, there are two epithelial folds on the lateral and two on the medial walls. These folds alternate in position and might serve as a closing mechanism. The pupa has only two median folds, one dorsal and one ventral. In the adult the lumen contains a neutral, granular secretion which is absent in the pupa.

The bound accessory gland duct is formed by the two accessory gland ducts held together by a common peripheral muscle coat. Anteriorly, the

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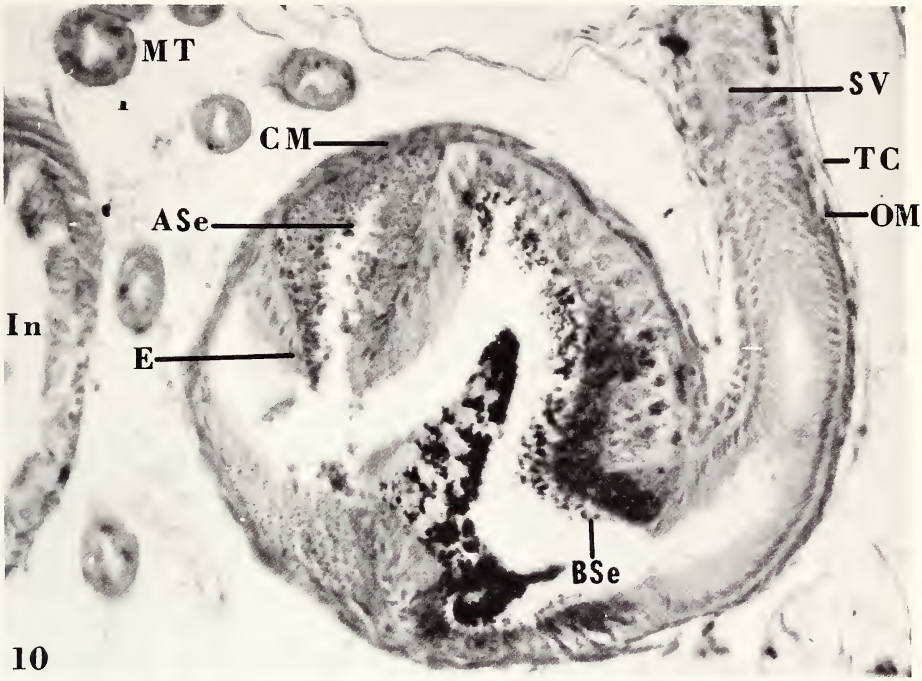
Figs. 10, 11. Photomicrographs of cross sections of organs in the adult of *A. gracilis*. 10. The accessory gland and the seminal vesicle opening into it. ×266. 11. The bound accessory gland duct. ×300.



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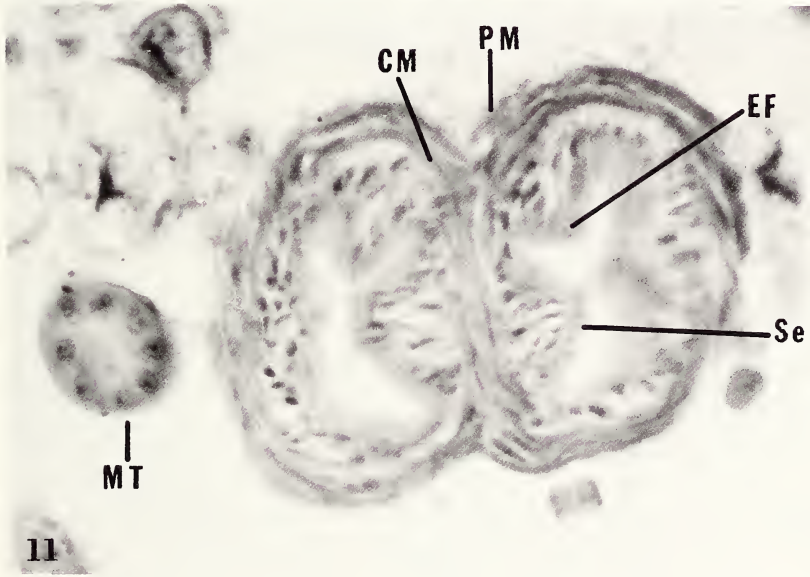

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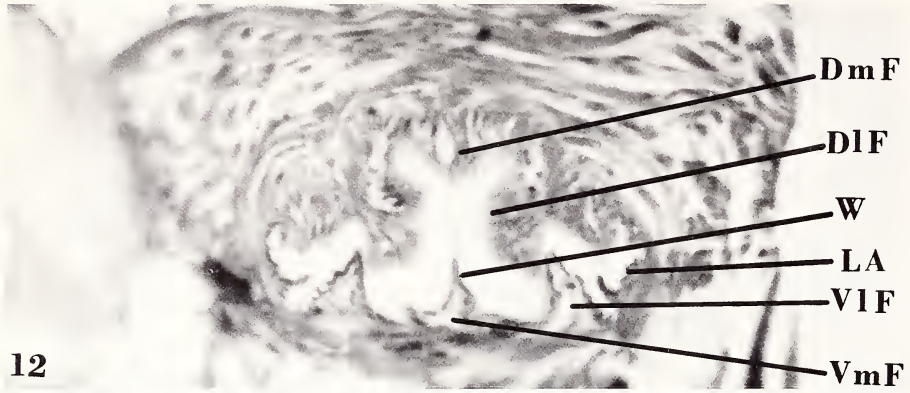
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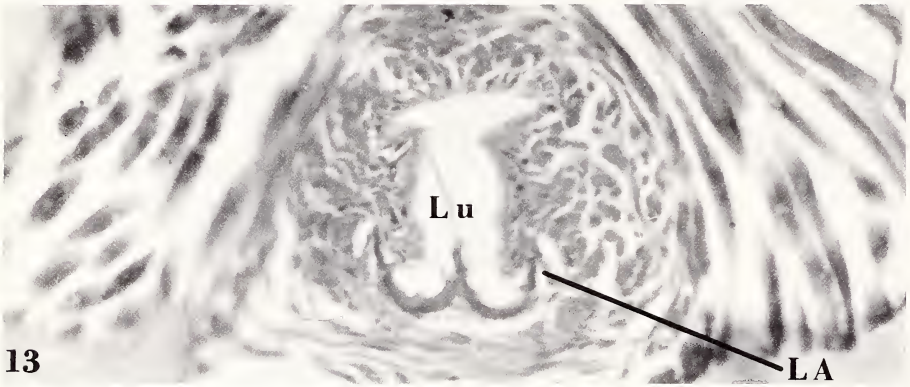
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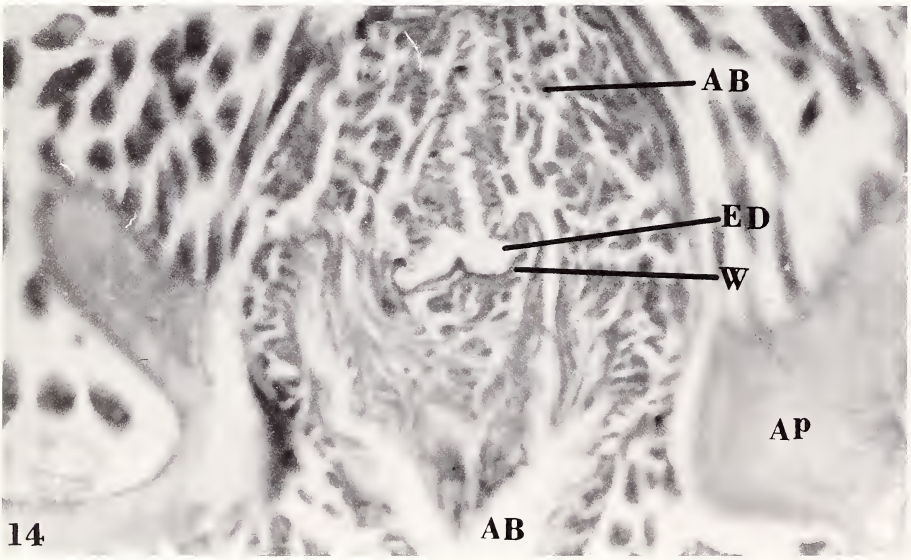
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epithelium in each duct has two folds, one dorsomedian and one ventromedian. The cells over these folds are columnar and the rest of the epithelium is cuboidal. Posteriorly, these folds gradually decrease in height and new folds are formed on the dorsal, lateral, and ventral walls. The lumina contain a neutrophilic, granular secretion. The muscle coat is composed of a few circularly arranged fibers around each accessory gland duct, and a few peripheral circular and oblique fibers that bind the two ducts together (Fig. 11). At the posterior end, the muscle fibers between the two ducts are reduced in number and disappear. The two lamina join into one and the duct formed is the ejaculatory duct. Histologically, the pupa is similar to the adult in this region.

The first part of the ejaculatory duct has two prominent dorsal folds and smaller lateral and ventral folds. The latter become more pronounced posteriorly. The columnar epithelium in this duct is taller over the folds. In the pupa, this region has narrow folds; three dorsal, two lateral, and one ventral. In the adult, the apices of the two dorsal folds become much broader, and, at this level, the formation of the cuticular wedge is first seen as a thin intima over the epithelium on the ventrolateral folds. The muscle coat consists of 2 or 3 inner oblique fibers and 1 or 2 outer circular fibers. More posteriorly, a fold is formed between the two dorsal folds, the small lateral folds broaden, and the ventral one becomes a tall narrow midventral fold. The cuticular wedge is now broadly W-shaped, thicker ventrally, and the lateral arms are thinner and wavy in appearance. In the pupa the wedge is short and is less complex in its structure. The muscle coat on the dorsal and lateral walls in the adult has increased by several fibers in thickness, and some of these fibers are longitudinally arranged (Fig. 12). In the pupa, the muscle fibers are not distinct and are being formed. Further along in the adult, the midventral portion of the wedge becomes thicker, broader for a short distance, and then narrows and extends upward into the lumen. The middorsal fold is reduced in height and disappears, and the midventral fold of the wedge lowers. The muscle coat becomes thicker laterally, and pushes the lateral folds inward. Toward the distal region, the lateral arms move mesially and the wedge is W-shaped (Fig. 13). The posterior tip of the wedge is thinner and flatter. The distal end of the ejaculatory duct extends through the dorsal wall of the aedeagal bladder at the level of the anterior region of the inner

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Figs. 12–14. Photomicrographs of cross sections through the ejaculatory duct and wedge in the adult of *A. gracilis*; all are magnified ×215. 12. This section is about at the midregion of the wedge and shows the extended lateral arms of the wedge. 13. This section shows the reduction of the lateral arms of the wedge, the formation of its base, and the laterally compressed lumen. 14. This section shows the end of the ejaculatory duct opening through the roof of the aedeagal bladder.

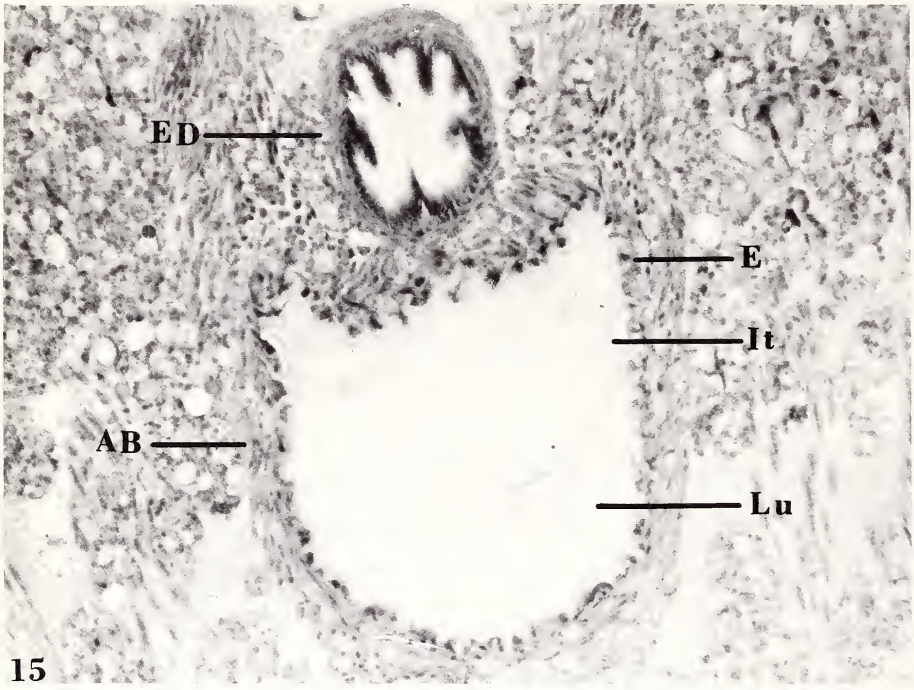

Fig. 15. Photomicrograph of cross sections through the ejaculatory duct and the aedeagal bladder in the pupa of *A. gracilis*. ×210.

valves (Fig. 14), and just beyond the end of the wedge the floor of the ejaculatory duct opens into the aedeagal bladder. The muscles of the dorsal and lateral walls of the ejaculatory duct are incorporated into the dorsal wall of the aedeagal bladder. The lumen of the duct throughout, in both adults and pupae, is devoid of any secretion.

The cuticular wedge on the ventral surface of the ejaculatory duct, referred to as the chitinous "penes" in *D. labiatus* by Mukerjee (1926) and described in detail by Clausen (1938) in formicine ants, is present in all male ants in which the histology has been described. The shapes of the wedges and the histological organization of the ejaculatory ducts exhibit differences in all male ants. In the origin of the arms of the wedge from the ventrolateral folds of the duct and in the formation of a ventral median ridge on the base, *A. gracilis* resembles the Old World dorylines.

The wall of the aedeagal bladder consits of a thick, wrinkled intima and an underlying epithelium of small cells with prominent spherical or ellipsoidal nuclei. The epithelium is surrounded by a thick muscle coat of large inner circular and outer obliquely arranged fibers; the latter are inserted on the median walls of the inner valves at their anterior ends. In the adult, the

dorsal and lateral walls in the anterior region of the bladder are deeply folded, and muscle fibers extend into these folds. In the pupa, the walls are not folded, the lumen is spacious (Fig. 15), and the dorsal wall is depressed in front of the point where the ejaculatory duct opens into the bladder. In the posterior region, in both the adult and the pupa, the intima is thin and not wrinkled, and there are small folds on the lateral walls. The lumen of the bladder opens between the inner valves. There is no secretion anywhere in the lumen of the aedeagal bladder.

Gotwald and Kupiec (1975), who analyzed the existing information on the morphology, behavior, and geographical distribution of the doryline tribes, indicate that the subfamily Dorylinae, as presently constituted, is triphyletic. The three lineages are the Ecitonini-Cheliomyrmecini, the Dorylini, and the Aenictini. They advocate the retention of the subfamily Dorylinae to include the tribe Dorylini and make a case for the creation of a subfamily Ecitoninae, already introduced by Brown (1973) to include the tribes Ecitonini and Cheliomyrmecini. The status of Aenictini, they conclude, remains to be determined by further investigation.

This report of the anatomy and histology of the reproductive system has brought to light several structures and features of phylogenetic importance. The larger number of testicular follicles, the histology of the testicular epithelium, the general structure of the accessory glands, the short straight bound accessory gland duct and ejaculatory duct, the formation of the chitinous wedge in the ejaculatory duct, and the structure of the genitalia are features in which *A. gracilis* is different from the New World dorylines. Some of these structures have been noted and described by Gotwald and Burdette (1981). It also differs from the Old World genus *Dorylus* subgenus *Anomma* in the presence of a capsule covering the testes, in the histology and secretion of the seminal vesicles, in the development of the wedge in the ejaculatory duct, in the entrance of the ejaculatory duct into the aedeagal bladder, in the absence of unicellular glands at the end of the ejaculatory duct and the aedeagal bladder, in the absence of a dorsal duct also at the end of the aedeagal bladder, and in the shapes of the genitalic valves and terminal sterna. These features exhibited by the male reproductive system in *Aenictus* lend support to the elevation of the tribe Aenictini to a subfamily rank, and to the triphyletic origin of the dorylines.

ABBREVIATIONS

A, anus; AB, aedeagal bladder; AG, accessory gland; AGD, accessory gland duct; Ao, aorta; Ap, apodeme; ASe, acidophilic secretion; B, basal cell layer; Br, brain; BR, basal ring; BSe, basophilic secretion; BT, buccal tube; CM, circular muscle; CS, campaniform sensilla; DlF, dorsolateral fold; DM, dilator muscle; DmF, dorsomedian fold; E, epithelium; ED, ejaculatory duct;

EF, epithelial fold; G1, G2, G3, G4, gastric ganglia; H, heart; I, inner cell layer; IC, infrabuccal chamber; In, intestine; It, intima; IV, inner genitalic valve; L, labium; LA, lateral arm; LP, lamina parameralis; Lu, lumen; M, mandible; MC, muscle coat; MG, mandibular gland; MP, median process; MT, Malpighian tubule; N, notch; Oc, ocellus; Oe, oesophagus; OL, optic lobe; OM, oblique muscle; OV, outer genitalic valve; Pa, paramere; PC, preoral cavity; Pe, petiole; PeG, petiolar ganglion; PG, postpharyngeal gland; Ph, pharynx; PM, peripheral muscle coat; R, rectum; RP, rectal pad or gland; RV, rectal valve; S, spermatozoa; SD, salivary duct; Se, secretion; SG, salivary gland; Sl, salivarium; SoG, suboesophageal ganglion; SV, seminal vesicle; T, testis; T1, T2, T3, thoracic ganglia; TC, testicular capsule; TF, testicular follicle; TP, triangular plate; V, vacuole; VE, vas efferens; VD, vas deferens; VlF, ventrolateral fold; VmF, ventromedian fold; Vn, ventriculus; VNC, ventral nerve cord; W, wedge; IX, 9th abdominal sternum; X, 10th abdominal tergum.

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